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A Review of the Genus *Berthella* (Opisthobranchia: Notaspidea) from the Pacific Coast of North America

by

TERRENCE M. GOSLINER AND HANS BERTSCH

Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

Abstract. Examination of specimens of *Berthella* from the Gulf of California and the Pacific coast of Baja California indicated morphological similarities with *B. stellata, B. pellucida,* and *B. tupala.* A detailed morphological review of specimens from the Mediterranean, Caribbean, Pacific, and Indian oceans revealed that all these taxa constitute a single, circumtropical species, *B. stellata.*

Specimens of *Berthella agassizii,* known previously only from the Caribbean and Brazil, are recorded from the Gulf of California and the Pacific coast of Baja California.

The morphology and systematics of three other species of *Berthella* from the northeastern Pacific are reviewed. The reproductive morphology of *B. californica* differs significantly from its original description. *Berthella kaniae* is regarded as a synonym of *B. martensi. Berthella strongi* was originally described as a *Pleurobranchus,* but all morphological features are consistent with *Berthella.* The genus *Pleurehdera* closely resembles *Berthella,* particularly in light of species examined in this study. Further study is required to assess its systematic position.

INTRODUCTION

Three species of the pleurobranchid genus *Berthella* Blainville, 1825, are currently known from the Pacific coast of North America. BERGH (1898) recorded *Berthella sideralis* (Lovén, 1847) from Unalaska. MACFARLAND (1966) stated that this record is dubious, in light of the fact that the buccal mass was absent from the mutilated specimen. No diagnostic characters that verify the identification were present. Therefore, there is no basis for considering this species as a member of the northeastern Pacific marine fauna. *Berthella californica* (Dall, 1900) was described from southern California. SPHON (1972) described *B. kaniae* from the Pacific coast of Mexico and Panama. Other specific and subspecific taxa have been erected in the genera *Berthella* and *Pleurobranchus,* such as *P. strongi* MacFarland, 1966, and will be discussed within this paper.

During 1984 and 1985 the California Academy of Sciences, the Centro de Investigaciones Científica y de Educación Superior de Ensenada, and Escuela Superior de Ciencias Marinas of the Universidad Autónoma de Baja California conducted three expeditions to Baja California. During these expeditions numerous opisthobranch specimens were collected. Included in these collections were specimens of two species of *Berthella.* One of these species resembles *B. stellata* (Risso, 1826), *B. pellucida* (Pease, 1860) and *B. tupala* Marcus, 1957. Two specimens, resembling the described morphology of *Berthella agassizii* (MacFarland, 1909), were collected from both coasts of Baja California. While comparing specimens of these taxa to other congeners, it was noted that several erroneous or incomplete descriptions had appeared in the literature. It therefore became necessary to review the members of the genus from the Pacific coast of North America, and to compare them to closely allied taxa in other temperate and tropical portions of the world.

DESCRIPTIONS

Berthella californica (Dall, 1900)

(Figures 1A, 2, 3)

Pleurobranchus californicus DALL, 1900:92.
Pleurobranchus chacei Burch, 1944: MACFARLAND, 1966:84.
Pleurobranchus californicus denticulatus MACFARLAND, 1966: 84, pl. 5, figs. 1–5, pl. 13, figs. 25–34, pl. 16, fig. 12.

Berthella californica (MacFarland, 1966): Lance, 1966:71.
Berthella denticulatus (MacFarland, 1966): Lee & Foster, 1985:442.

Distribution: Point Craven, Alaska to Point Loma, San Diego County, California (Behrens, 1980; Lee & Foster, 1985).

Material: One specimen, California Academy of Sciences, San Francisco, CASIZ 064823, Point Pinos, Monterey, 36°38′N, 121°56′W, F. M. MacFarland. One specimen, intertidal zone, Duxbury Reef, Bolinas, Marin County, California (37°53′N, 122°42′W), June 1968, T. M. Gosliner. One specimen, CASIZ 064824, intertidal zone, Point Pinos, Pacific Grove, Monterey County, California, June 1947, F. Pitelka.

External morphology: The color of the living specimen from Duxbury Reef closely resembles that depicted by MacFarland (1966) and Behrens (1980). The body is translucent white with numerous, scattered opaque white spots and marginal notal band (Figure 1A). The ctenidium is simply plicate without tubercles along the rachis.

Internal morphology: The calcified portion of the shell was completely dissolved in the specimens we examined. Its structure has been well documented by MacFarland (1966).

The jaws are armed with numerous elements bearing 0–4 denticles on either side of the prominent central cusp (Figure 2A). The radular formula in two specimens was 63 × 63·0·63 and 95 × 75·0·75. The inner lateral teeth (Figure 2B) are simple, hook-shaped, without basal denticles. Towards the outer margin of the radula, the teeth are more elongate (Figures 2C, D).

The reproductive system (Figure 3) was well developed in the fully mature specimen from Monterey. The description of its morphology is based primarily on the dissection of that specimen. The ampulla is thick and muscular. Proximally, it narrows into the postampullary duct, where it divides into the oviduct and vas deferens. The oviduct is short and enters the female gland mass. Adjacent to the ampulla, but not connecting with it, is the pyriform receptaculum seminis. From its proximal end a narrow duct curves distally and joins the vaginal duct near its juncture with the large, spherical bursa copulatrix. The vaginal duct is thick and convoluted. It exits at the genital atrium. The nidamental glands are well developed, but could not be differentiated, owing to poor preservation of that part of the reproductive system. The glands open into the genital atrium. From the division of the postampullary duct the vas deferens expands into a thick, convoluted prostatic portion. A simple penial gland enters the proximal end of the prostatic vas deferens. More proximally the vas deferens narrows into a muscular ejaculatory segment, consisting of numerous convolutions. From the proximal end of the vas deferens a large muscular penis emerges.

Discussion: MacFarland (1966) described *Pleurobranchus californicus denticulatus* as a distinct subspecies, based on the fact that specimens possess denticles on the jaw platelets. Both *P. californicus* and *P. californicus denticulatus* were transferred to *Berthella* (Roller, 1970), since they lack prominent tubercles on the rachis of the ctenidium. Most recent workers (Behrens, 1980; Willan, 1984) have considered *B. californica denticulata* as a synonym of *B. californica*. The fact that in the present material the jaw elements may or may not have denticles, even within different portions of the jaw of a single specimen, further supports this view. Furthermore, there is no geographical separation of specimens with and without denticles.

MacFarland (1966:pl. 16, fig. 12) described the reproductive anatomy of *Berthella californica denticulata*. He depicted a system without a receptaculum seminis and with the bursa copulatrix connecting directly to the oviduct. Examination of material in this study revealed that a receptaculum seminis is indeed present. Also, the oviduct enters the female gland mass near the albumen gland, rather than joining with the bursa copulatrix. The configuration observed in the present material is consistent with that found in other species of *Berthella*.

Berthella martensi (Pilsbry, 1896)

(Figures 1B, C, 4–6)

Pleurobranchus scutatus Martens in Möbius, 1880:309, pl. 21, fig. 8 (*non* Forbes, 1844).
Bouvieria scutata (Martens in Möbius, 1880): Vayssière, 1896:123, pl. 5, figs. 16–18.
Gymnotoplax martensi Pilsbry, 1896:211, pl. 48, figs. 34, 35.
Berthella martensi (Pilsbry, 1896): Willan, 1984, figs. 8–12, 21–28, 30–32, 40–42, 44.
Berthella kaniae Sphon, 1972:53, figs. 1–9; syn. nov.

Distribution: This species is known in the Indo-Pacific tropics from Mauritius, Western Australia, eastern Australia, Fiji, Enewetak, and Hawaii (Willan, 1984) and from the eastern Pacific from Baja California Sur to Panama (present study).

Material: Two specimens, Los Angeles County Museum, AHR 454-35, tidal flats, Secas Islands, Panama (7°57′N, 82°00′45″W), 6 Feb. 1935, Allan Hancock Foundation. One specimen, 7 m depth, Las Arenas, Gulf of California, Baja California Sur, Mexico (24°02′N, 109°49′W), 16 June 1985, H. Bertsch. Two specimens, CASIZ 064828, 20 m depth, Bomber Reef, Madang, Papua New Guinea (5°15′S, 145°45′E), 27 Oct. 1986, J. Darr. One specimen, CASIZ 064829, 30 m depth, northern pass, Madang, Papua New Guinea, 2 October 1986, T. Frohm.

External morphology: The living animals reach 50 mm in length. They exhibit considerable variation in coloration. In the Mexican and Panamanian specimens, the ground color was off-white with scattered light brown spots (Figure 1B). This color pattern closely resembles that shown by Willan (1984:fig. 21) for a specimen from Enewetak. Two of the specimens collected from Papua New Guinea

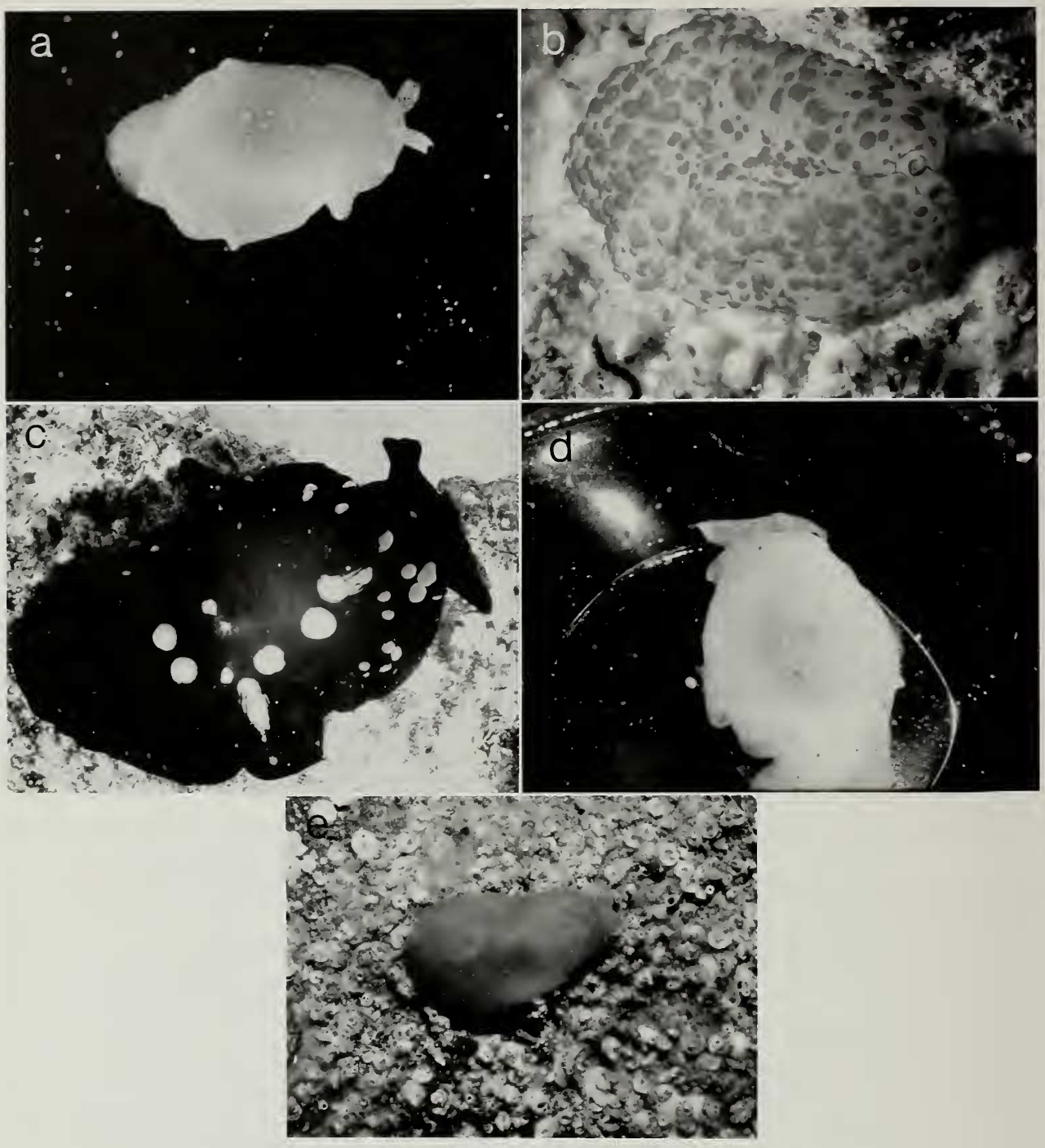

Figure 1

Living animals. A. *Berthella californica* (Dall, 1900), Duxbury Reef, Marin County, California, June 1968, photo by T.M.G. B. *Berthella martensi* (Pilsbry, 1896), Las Arenas, Baja California, 16 June 1985, photo by H.B. C. *Berthella martensi* (Pilsbry, 1896), Madang, Papua New Guinea, 2 October 1986, photo by T.M.G. D. *Berthella strongi* (MacFarland, 1966), Moss Beach, San Mateo County, California, 2 August 1966, photo by T.M.G. E. *Berthella agassizii* (MacFarland, 1909), Campitos, Punta Eugenia, Pacific coast of Baja California Sur, 30 June 1984, photo by T.M.G.

Figure 2

Berthella californica (Dall, 1900). Scanning electron micrographs. A. Jaw platelets, ×1100. B. Radular teeth from rachis, ×1500. C. Middle radular teeth, ×1500. D. Outer lateral teeth, ×1500.

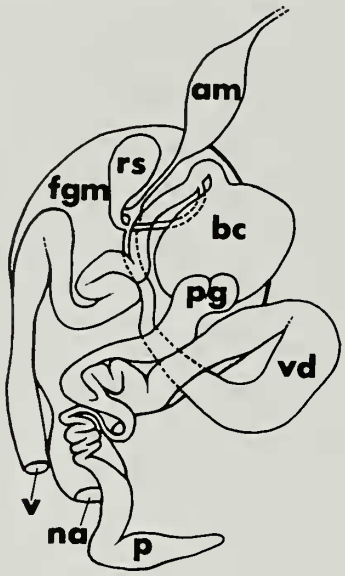

Figure 3

Berthella californica (Dall, 1900). Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; na, nidamental aperture; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

are orange with dark brown lines and spots (Figure 1C), similar in pattern to that depicted by WILLAN (1984:fig. 25) from the Great Barrier Reef. The largest specimen examined in this study, collected in Papua New Guinea, was dark brown with lighter brown tubercles. The Panamanian specimens and the largest specimen from Papua New Guinea have autotomized portions of the mantle. The ctenidium is large, tripinnate, with 18–20 primary pinnae on either side of the rachis. The anus is located dorsal to the posterior limit of the attached portion of the ctenidium.

Internal morphology: The calcified portion of the shell was dissolved by fixative in all material we examined.

The jaws are well developed with numerous minute elements. The jaw elements (Figure 4) are most commonly unarmed, but in one of the Panamanian specimens a single denticle was present on some elements.

The radular formula was 58 × 62·0·62 in the animal from the Gulf of California and 83 × 95·0·95 in one of the Panamanian specimens. The inner teeth (Figure 5A) are simple and hook-shaped. A single basal denticle is present on some of the inner 10 teeth but is absent in others (Figure 5B). The central teeth are simple and elongate, becoming more hook-shaped towards the outer margin (Figures 5C, D).

The reproductive system (Figure 6) is androdiaulic. Its morphology was identical in one specimen from Panama and one from Papua New Guinea. The ampulla is elongate, curved, and muscular. It divides distally into the short oviduct and the vas deferens. The oviduct enters the female gland mass near the albumen gland. The vas deferens is glandular for most of its length, but does not expand into a thickened prostatic gland. Near its distal end it joins with the elongate, curved penial gland and narrows into a short ejaculatory segment prior to entering the penial sac. The pyriform receptaculum seminis and the spherical bursa copulatrix join the vaginal duct near the middle of its length. The vaginal opening is immediately ventral to the penis.

Discussion: The variability of the living animal and the anatomy of *Berthella martensi* were recently reviewed (WILLAN, 1984). One of the chief distinguishing features of this species is the presence of "preformed shear zones" where portions of the mantle may be autotomized. In his discussion of this species, Willan noted that *B. kaniae* Sphon, 1972, also autotomizes portions of its mantle. Willan suggested that it differs from *B. martensi* in not having distinct shear zones and in having a more shallowly cleft anterior margin of the mantle. However, specimens examined in this study indicate that Panamic specimens also have preformed areas where autotomy occurs. Similarly, the mantle is as deeply cleft in these specimens as in Willan's figures (1984:figs. 21–25) of *B. martensi*. The jaws and radula of the present material agree well with those described for *B. martensi*. Willan noted that *B. martensi* lacks a vas deferens expanded into a distinct prostate gland. The present material also lacks a distinct prostate. There is no basis for maintaining the separation of *B. kaniae* Sphon, 1972, and it is here regarded as a junior synonym of *B. martensi* (Pilsbry, 1896).

Berthella stellata (Risso, 1826)

(Figures 7–12)

Pleurobranchus stellatus RISSO, 1826:41.
Berthella stellata (Risso, 1826): PRUVOT-FOL, 1954:223.
Pleurobranchus pellucidus PEASE, 1860:24; syn. nov.
Berthella pellucida (Pease, 1860): THOMPSON, 1970:188; syn. nov.
Berthella tupala ER. MARCUS, 1957:416, figs. 58–69; syn. nov.
Berthella postrema Burn, 1962: WILLAN, 1984:42.
Berthella stellata albocrossata HELLER & THOMPSON, 1983: 328, figs. 5A–C; syn. nov.

Distribution: *Berthella stellata* was originally described from the Mediterranean (RISSO, 1826; THOMPSON, 1981). It has also been recorded from the Indo-Pacific tropics from South Africa (GOSLINER, 1987, as *B. tupala*), the Sudanese Red Sea (HELLER & THOMPSON, 1983, as *B. stellata albocrossata*), Australia (BURN, 1962, as *B. postrema*; THOMPSON, 1970, and WILLAN, 1984, as *B. pellucida*), New Caledonia (RISBEC, 1928, as *B. pellucida*) and Hawaii (PEASE, 1860, and KAY, 1979, as *B. pellucida*). In the eastern Pacific this species occurs from the Pacific coast of Baja California and from several localities within the Gulf of California (present study). The species has been recorded from several localities within the Caribbean (as *B. tupala*): Brazil (ER. MARCUS, 1957); Florida (EV. MARCUS

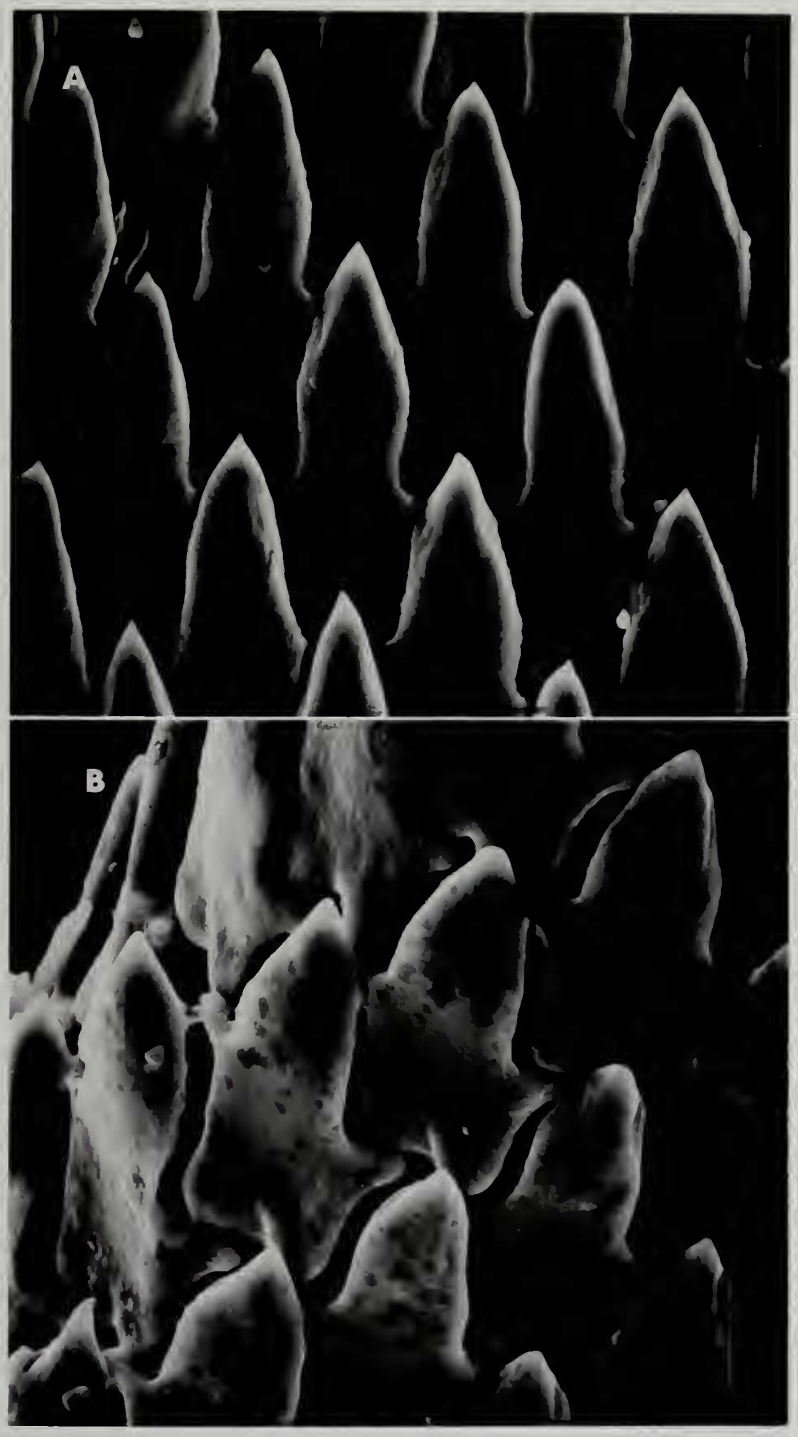

Figure 4

Berthella martensi (Pilsbry, 1896). Scanning electron micrographs of jaw platelets from different portions of the same jaw of the specimen from Las Arenas. A. ×1300. B. ×1500.

Figure 5

Berthella martensi (Pilsbry, 1896). Scanning electron micrographs of radula. A. Dorsal view of rachis of Las Arenas specimen, ×1700. B. Lateral view of rachis of Panamanian specimen, ×1300. C. Middle lateral teeth of Panamanian specimen, ×1000. D. Outer lateral teeth of Las Arenas specimen, ×1700.

& Er. Marcus, 1967); Puerto Rico (Er. Marcus & Ev. Marcus, 1970a); Panama (Bertsch, 1975); Colombia (Ev. Marcus, 1984). We report its occurrence from the Caribbean, Gulf of California, and Pacific coasts of Mexico. Thus, *B. stellata* has a circumtropical distribution.

Material: Two specimens, California Academy of Sciences, San Francisco, CASIZ 064827, intertidal zone, Fokea, Greece, 13 June 1986, T. E. Thompson. One specimen, CASIZ 063274, 1 m depth, eastern shore of Laguna de Nichupte, Cancun, Quintana Roo, Mexico (21°25′N, 86°50′W), 2 January 1978, T. M. Gosliner. One specimen, CASIZ 064832, 7 m depth, W side of point of Fort Jeudy, Grenada (11°59′N, 61°42′W), 24 August 1986, H. Bertsch. One specimen, CASIZ 063277, intertidal zone, Centro de Acuacultura, Bahía Tortugas, Baja California Sur, Mexico (27°42′N, 114°53′W), 2 July 1984, H. Bertsch. One specimen, CASIZ 064834, Isla Coronado, Bahía de los Angeles, Baja California, Mexico (29°03′N, 113°31′W), 27 April 1986, H. Bertsch. One specimen, CASIZ 064830, 10 m depth, Punta Gringa, Bahía de los Angeles, Baja California, Mexico, 29 June 1987, S. Millen. One specimen, CASIZ 064825, 3 m depth, El Embudo, Isla Partida, Baja California Sur, Mexico (24°32′N, 110°23′W), 23 July 1985, T. M. Gosliner. One specimen, CASIZ 063275, under rock in seawater tables, Hawaii Institute of Marine Biology, Coconut Island, Oahu, Hawaiian Islands (21°32′N, 157°40′W), 26 October 1986, T. M. Gosliner. One specimen, CASIZ 064833, intertidal zone, under rocks, Hastings Point, New South Wales, Australia, October 1986, R. C. Willan and T. M. Gosliner. One specimen, South African Museum, Cape Town, SAM A35259, intertidal zone, under large rock, Umgazana, Transkei, South Africa (31°37′S, 29°32′E), 28 October 1981, T. M. Gosliner.

External morphology: The living animals examined in this study (Figure 7) reached a maximum length of 20 mm. The body is generally translucent white to honey brown. Scattered, small opaque white markings are present on the notum. An opaque white transverse bar or cross is generally situated near the middle of the notum, but may be entirely absent in specimens from several localities. In one specimen collected by one of us (H.B.) from Puerto Peñasco, Mexico, a yellow tubercle was present on either limit of the opaque white transverse bar. The ctenidium is bipinnate with up to 17 primary pinnae on either side of the rachis. The anus is situated dorsal to the posterior limit of the gill membrane.

Internal morphology: The shell (Figure 8) is elongate with faint to well developed longitudinal and axial sculpture.

The jaws are strongly developed with numerous chitinous elements (Figure 9). The shape and dentition of these elements vary considerably, even within a single jaw (Figures 9E, F, Table 1). There are 1–6 denticles on either side of the jaw elements in the present material.

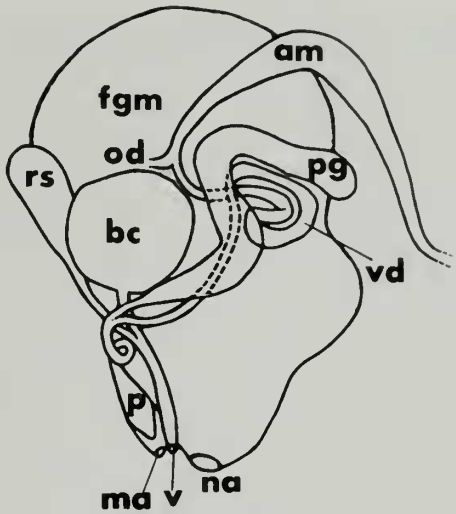

Figure 6

Berthella martensi (Pilsbry, 1896). Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; od, oviduct; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

The radular formula exhibited considerable variation in the individual specimens examined in this study (Table 1). The combined formula is 50–80 × 45–72·0·45–72. The inner lateral teeth are simple and hook-shaped (Figure 10). A basal denticle is present on some of the inner teeth in specimens from Cancun (Mexico) and Umgazana (South Africa) (Figure 10C). The length of the cusp of the radular teeth increases towards the margin. In all specimens the outer 4–10 lateral teeth are elongate and possess a secondary denticle, in addition to the main cusp (Figure 11). In the specimen from Bahía de los Angeles and the animals from Greece, the outermost teeth are not elongate, but still have a secondary denticle.

The reproductive system (Figure 12) is androdiaulic. The ampulla is elongate and curved, but not convoluted. It bifurcates distally into a short oviduct and the vas deferens. The oviduct enters the female gland mass near the albumen gland. The vas deferens expands into a thickened prostate and narrows again distally, just prior to its juncture with the penial gland. The penial gland is shortest in the specimen from Cancun and most elongate and convoluted in the Hawaiian specimen. The penis is short and muscular. The receptaculum seminis is pyriform and lightly pigmented in all specimens examined. The duct of the receptaculum seminis may be short or elongate, and may enter the vaginal duct at the base of the spherical bursa copulatrix or near the middle of the vagina. The vaginal duct exits immediately ventral to the penis.

Discussion: Several species of *Berthella* with scattered or medially situated opaque white markings have been considered as distinct for many years (Risso, 1826; Pease, 1860; MacFarland, 1909; Er. Marcus, 1955, 1957;

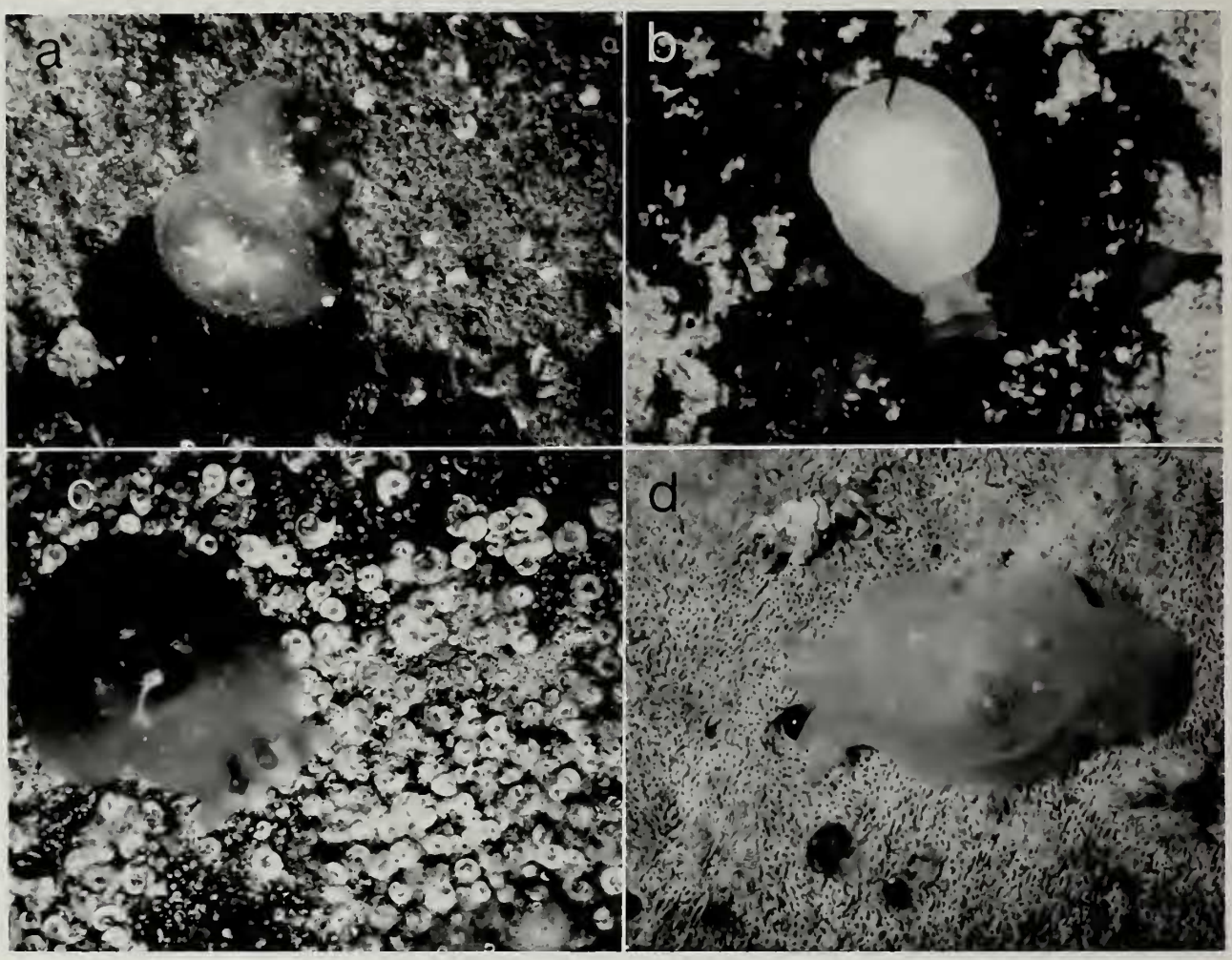

Figure 7

Berthella stellata (Risso, 1826). Living animals. A. Specimens from Puerto Peñasco, Sonora, Gulf of California coast of Mexico. B. Specimen from Umgazana, Transkei, South Africa. C. Specimen from Bahía Tortugas, Baja California Sur, Pacific coast of Mexico. D. Specimen from Hastings Point, New South Wales, Australia.

Thompson, 1981; Heller & Thompson, 1983; Ev. Marcus, 1984). Bertsch (1975) and Willan (1984) have shown that certain characters, particularly the elaboration of jaw elements, may vary considerably within single populations or individuals of *Berthella* species.

In attempting to identify specimens of *Berthella* from various localities on both coasts of Baja California, it became apparent that a critical review of species with similar markings was necessary to establish the identity of this material. Material from the Aegean Sea of Greece, the western Atlantic of Mexico, Grenada and Brazil, the Hawaiian Islands, Australia, and South Africa was examined in addition to the Baja Californian material. Table 1 indicates the range of morphological variability present in material examined in this study and known from the literature.

The color of specimens varies greatly. In almost all cases the body is translucent whitish to yellowish brown. The presence or absence of opaque white pigment and its variable arrangement has been noted by numerous authors. Thompson (1985; personal communication) has documented considerable variability in the arrangement of opaque white pigment of Aegean specimens. He also noted that occasional yellow tubercles may be present, as in the specimen from Puerto Peñasco described above.

The anus is always situated at the posterior end of the gill membrane.

The shell of *Berthella stellata* in all material, when preserved, is well developed with faint to well developed sculpture. The length relative to the width, though not quantified, varies considerably.

The shape and denticulation of the jaw elements varies markedly. There is significant variation even between different portions of a single jaw (Figures 9E, F). Willan

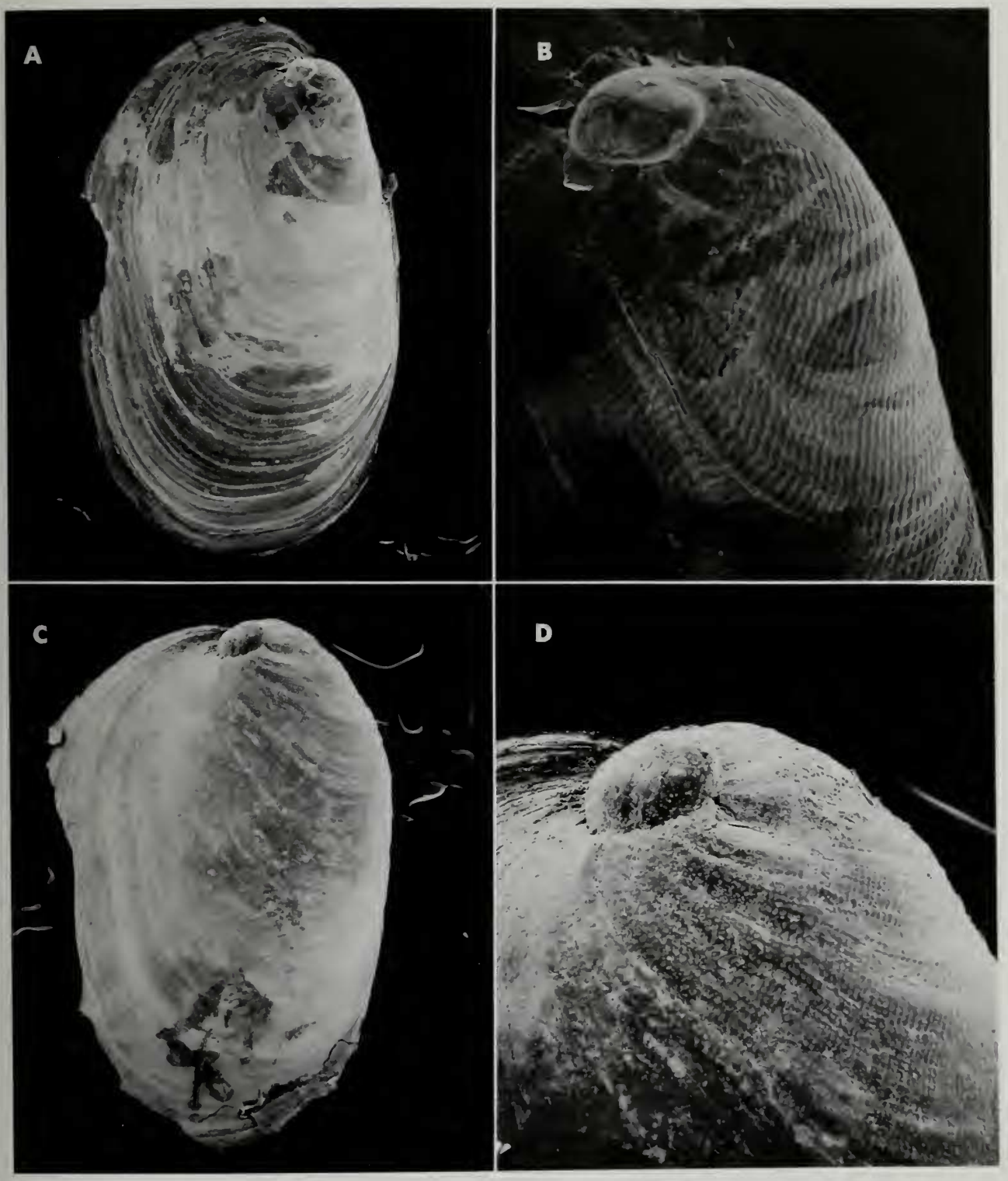

Figure 8

Berthella stellata (Risso, 1826). Scanning electron micrographs of shells with detail of sculpture and protoconch. A. ×22. B. ×100, specimen from Bahía Tortugas, Baja California Sur, Pacific coast of Mexico. C. ×25. D. ×70, specimen from Coconut Island, Oahu, Hawaiian Islands.

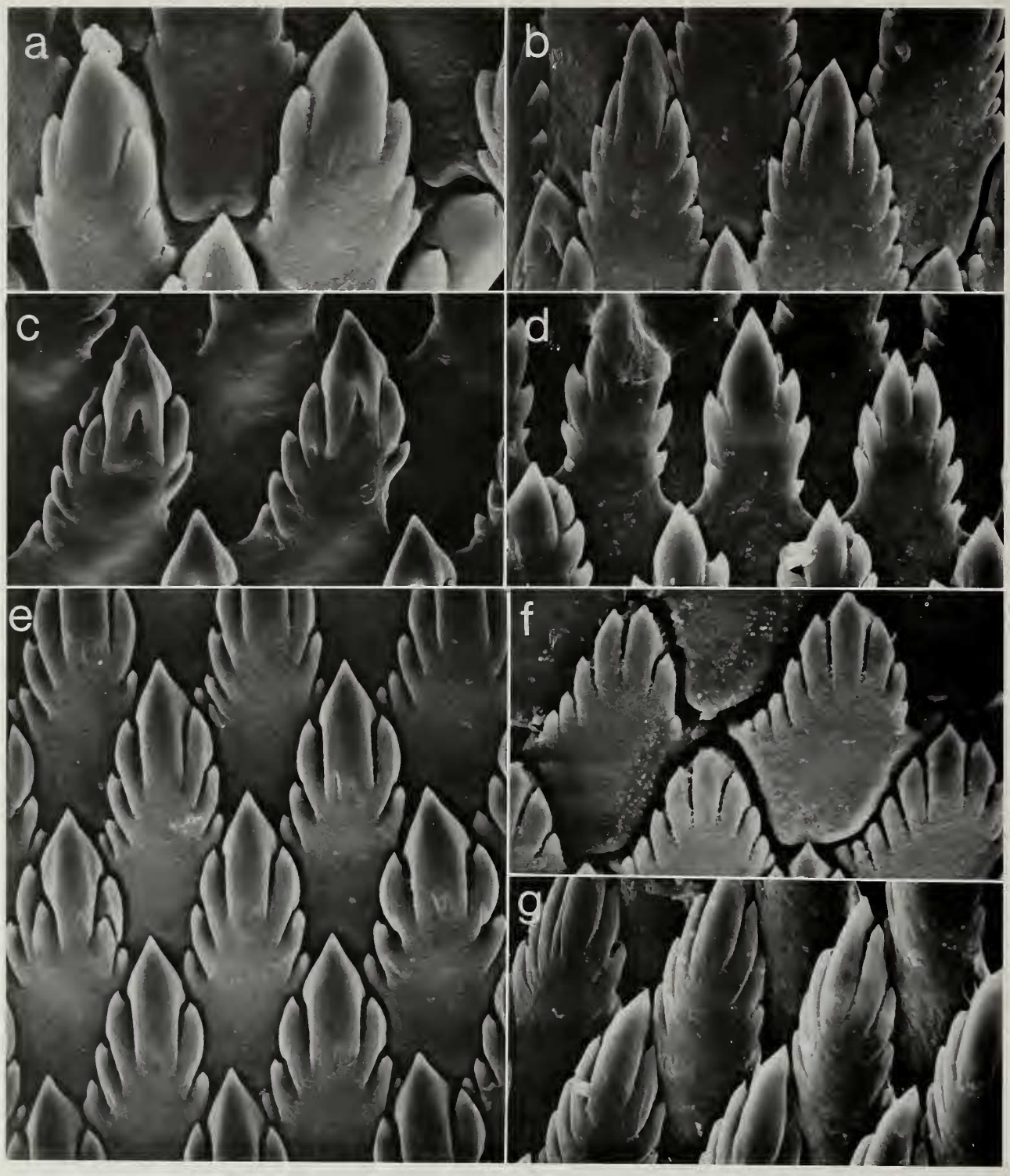

Figure 9

Berthella stellata (Risso, 1826). Scanning electron micrographs of jaw platelets. A. Small specimen from Fokea, Greece, ×1700. B. Large specimen from Fokea, Greece, ×1000. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico, ×1700. D. Specimen from Bahía de los Angeles, Baja California, Gulf of California coast of Mexico, ×1500. E and F. Different portions of same jaw of specimen from Coconut Island, Oahu, Hawaiian Islands, both ×2000. G. Specimen from Hastings Point, New South Wales, Australia, ×1480.

Table 1

Morphological variability in *Berthella stellata*.

Specimen	Color	Shell	Radular formula	Inner laterals	Outer laterals	Receptaculum seminis	Jaw denticle	Entrance of rs duct into vagina	Locality	Reference
Berthella tupala	ochre with opaque white trapezoid and spots	broad, with moderate sculpture	55 × 50·0·50	denticle on inner tooth	6–8 outer teeth bifid	absent	0–5	—	Brazil	MARCUS, 1957, 1967; MARCUS & MARCUS, 1970a
B. tupala	yellowish with opaque white "T"	broad, with distinct sculpture	—	1st three laterals with basal denticle	—	—	0	—	Panama	BERTSCH, 1975
B. pellucida	pale honey brown with opaque white cross and/or spots	broad, without marked sculpture	57 × 55·0·55 61 × 58·0·58 60 × 45·0·45	simple hooks, no dentricles	some bifid	no pigment noted	—	base of bursa	Enewetak, Marshall Is.	WILLAN, 1984
B. stellata	translucent white with scattered opaque white spots	broad, with moderate sculpture	56 × 49·0·49	no denticles	outer 9–10 teeth bifid	light	1–5	base of bursa	Hawaii	present study
B. stellata	translucent white with opaque white bar	dissolved	50 × 55·0·55	some denticles	bifid	light	1–5	middle of vagina	Cancun	present study
B. stellata	translucent white with scattered opaque white spots	narrow, with sculpture	57 × 59·0·59	no denticles	bifid	light	2–5	middle of vagina	Bahía Tortugas, Pacific coast Baja Calif.	present study
B. stellata	—	dissolved	61 × 61·0·61	no denticles	some bifid	light	2–5	into middle of vagina	Bahía de Los Angeles, Gulf coast of Baja Calif.	present study
B. tupala	translucent white with opaque white bar and scattered spots	broad, with moderate sculpture	54 × 61·0·61	some denticles	bifid	light	0–5	—	South Africa	GOSLINER, 1987
B. stellata	white ? honey with opaque white spots	faint sculpture	65 × 54·0·54 72 × 63·0·63	no denticles	some bifid	light	2–5	base of bursa	N.S.W., Australia	present study
B. stellata	whitish with opaque white	faint sculpture	58 × 62·0·62 72 × 62·0·62	—	—	—	—	—	Yugoslavia	THOMPSON, 1985
B. stellata albocrossata	off-white with opaque white cross	absent	51 × 51·0·51	—	—	—	4	—	Sudanese Red Sea	HELLER & THOMPSON, 1983
B. stellata	—	faint sculpture	52 × 57·0·57 80 × 72·0·72	no denticles	some bifid	light	2–6	middle of vagina	Greece	present study

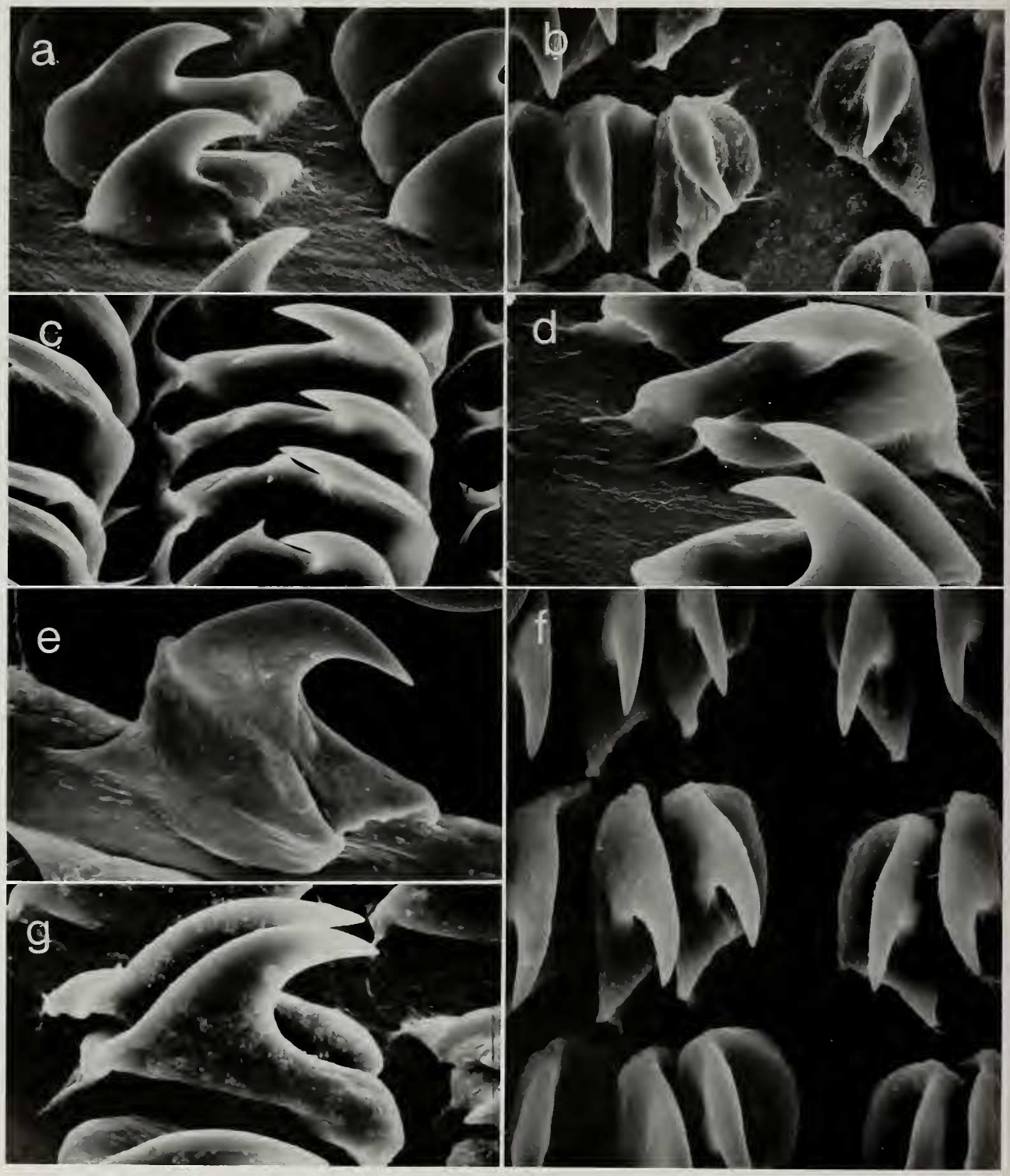

Figure 10

Berthella stellata (Risso, 1826). Scanning electron micrographs of rachis and innermost teeth. A. Small specimen from Fokea, Greece, ×2500. B. Large specimen from Fokea, Greece, ×1700. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico, ×3500. D. ×3000. E. Specimens from Bahía de los Angeles, Baja California, Gulf of California coast of Mexico, ×2000. F. Specimen from Hastings Point, New South Wales, Australia, ×2000. G. Specimen from Coconut Island, Oahu, Hawaiian Islands, ×5000.

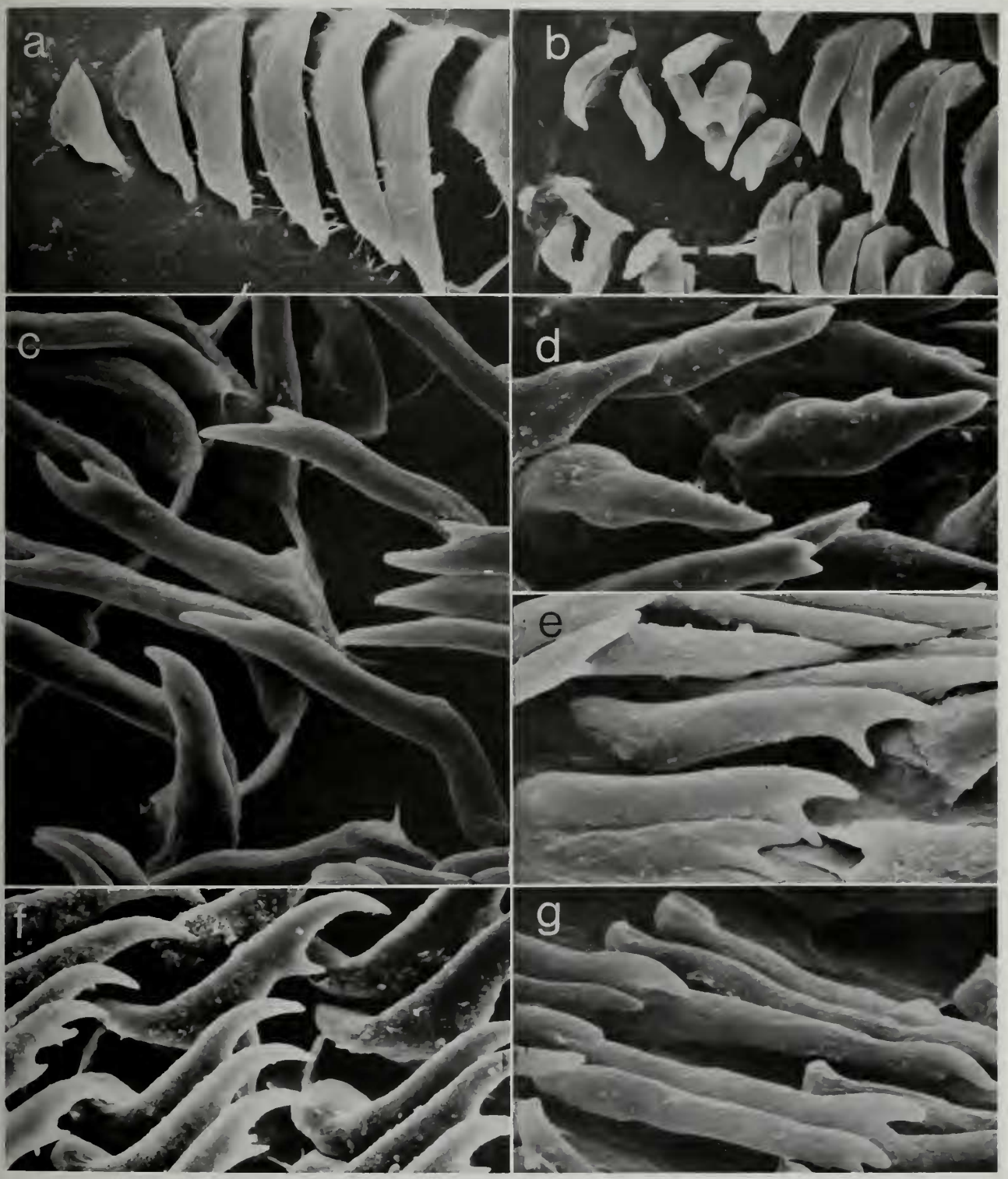

Figure 11

Berthella stellata (Risso, 1826). Scanning electron micrographs of outermost radular teeth. A. Small specimen from Fokea, Greece, ×2200. B. Large specimen from Fokea, Greece, ×1500. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico, ×3000. D. Specimen from Bahía de los Angeles, Baja California, Gulf of California coast of Mexico, ×2000. E. Specimen from Bahía Tortugas, Baja California Sur, Pacific coast of Mexico, ×4000. F. Specimen from Coconut Island, Oahu, Hawaiian Islands, ×2500. G. Specimen from Hastings Point, New South Wales, Australia, ×2500.

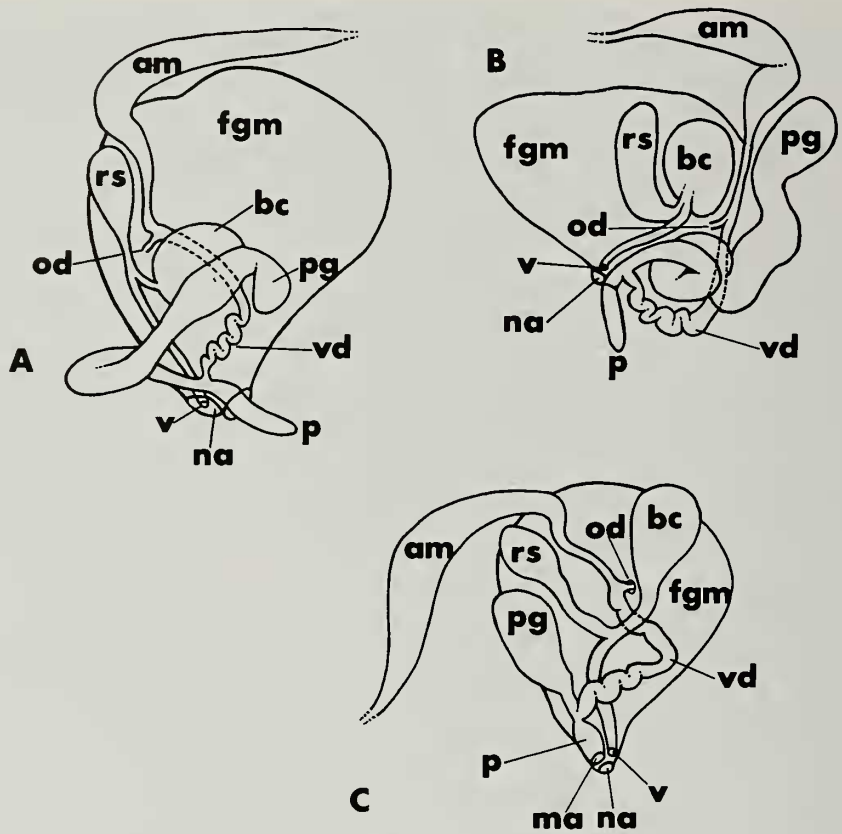

Figure 12

Berthella stellata (Risso, 1826). Reproductive systems. A. Specimen from Fokea, Greece. B. Specimen from Coconut Island, Oahu, Hawaiian Islands. C. Specimen from Cancun, Quintana Roo, Caribbean coast of Mexico. Key: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; od, oviduct; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

(1984) noted the variability in the number of denticles of jaw elements of various species of *Berthella,* including *B. pellucida* and *B. tupala.* None of the material examined in the present study entirely lacked denticles.

The radular formula varied slightly in all accounts. Considerable variation was present, however, in the shape and secondary denticulation of the inner and outer radular teeth. In all specimens, the inner teeth are short and hook-shaped. On some teeth there is a secondary denticle, but this is inconsistent even within a single individual. The teeth are more elongate towards the outer margin, and a secondary denticle is present on the cusp of the outer teeth, in all material examined.

The reproductive morphology is uniform throughout the material studied, with a few minor exceptions. The duct of the receptaculum seminis may join the vagina at the base of the bursa copulatrix, or near the middle of the vaginal duct (Table 1). The length of the penial gland also varies slightly.

Studies on the systematics of *Berthella* have focused on minute differences between species. This is particularly true of material described from the Caribbean (Ev. Marcus, 1984). Part of the confusion stems from the fact that several species have been incompletely or incorrectly described. The reproductive anatomy of *B. stellata* has never been described. The description of *B. tupala* (Er. Marcus, 1957) indicates that a receptaculum seminis is absent and that the uterine duct enters the female gland mass. No other known species lacks a receptaculum seminis or has any connection of either the receptaculum or bursa copulatrix directly with the female gland mass. The fact that the specimen from Cancun examined in this study agreed with Marcus' description of *B. tupala,* but had a more typical arrangement of reproductive organs, with a receptaculum seminis, suggests that the original description of the arrangement of reproductive organs was in error.

When one examines the morphological variability of these species of *Berthella* (Table 1) several facts become apparent. (1) Much of the variation exhibited throughout the world is expressed in individuals within a single limited geographical area, such as Baja California. (2) There is

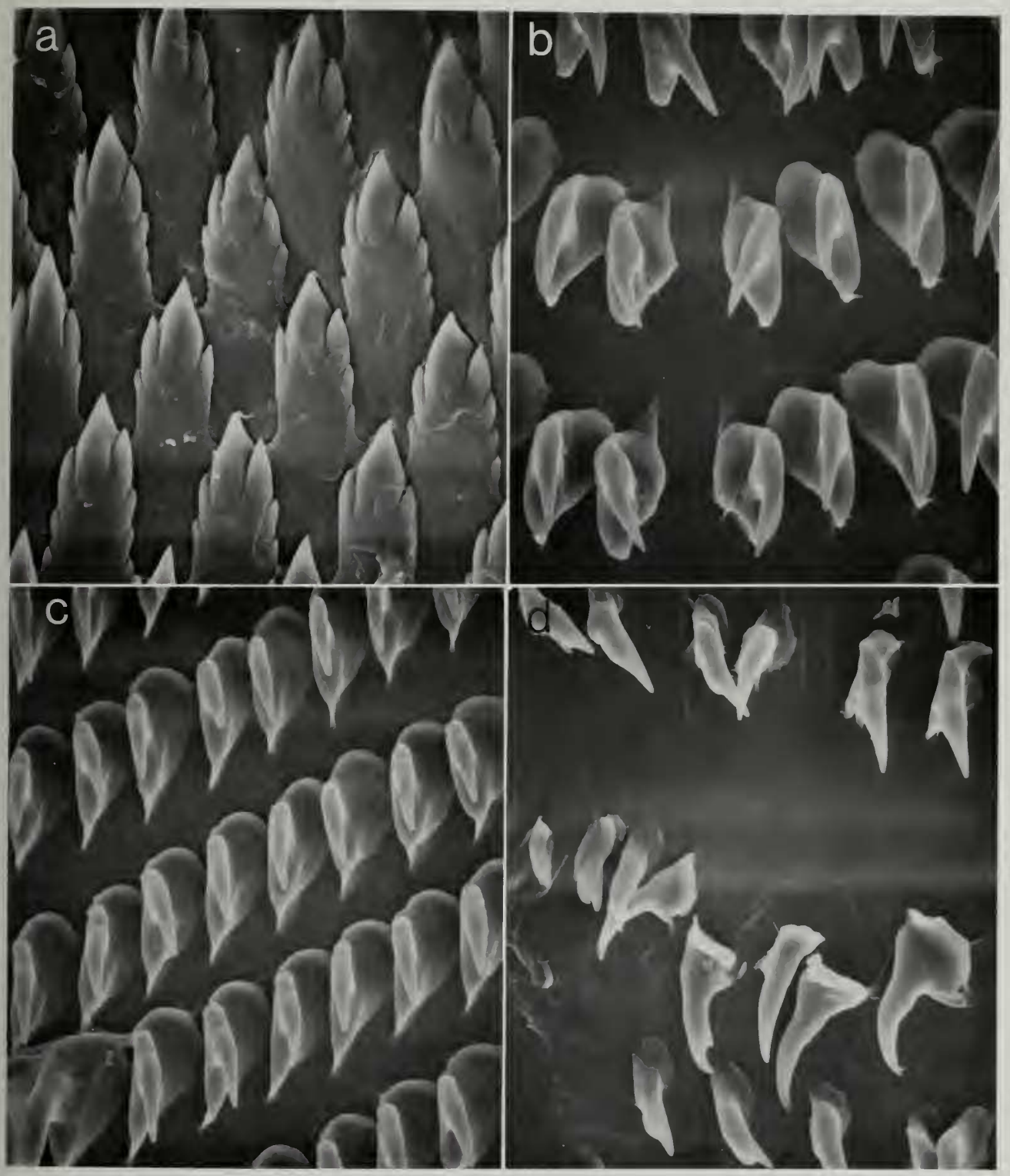

Figure 13

Berthella strongi (MacFarland, 1966). Scanning electron micrographs. A. Jaw platelets, ×1190. B. Rachis of radula, ×1700. C. Middle of radula, ×1300. D. Outer radular teeth, ×3000.

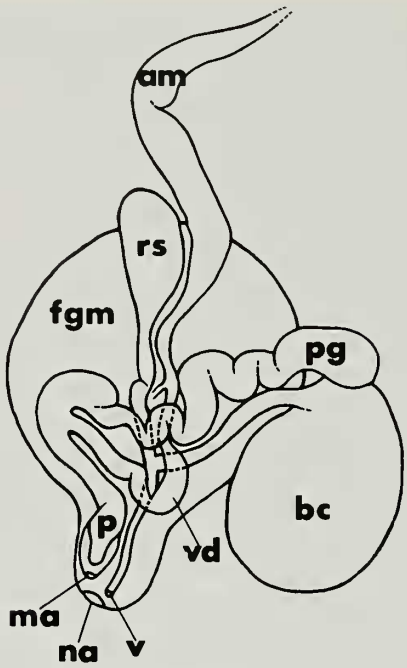

Figure 14

Berthella strongi (MacFarland, 1966). Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

little consistency in the correlation of variable characters. (3) There is little correlation between morphological variability and specific geographical regions.

Based on these facts one can arrive at several conclusions. (1) Each variant with a different set of characters must be considered as a distinct species. (2) Several species are widespread and are often sympatric. (3) Only one variable, circumtropical species exists. It is far more parsimonious and biologically realistic to consider *Berthella pellucida* (and its synonyms listed by WILLAN, 1984), *B. tupala,* and *B. stellata albocrossata* all as junior synonyms of *B. stellata.*

Berthella tamiu Ev. Marcus, 1984, is also found from the Caribbean, though from deeper water than *B. stellata.* It differs from *B. stellata* in several important regards. All of the jaw elements are edenticulate. The radula contains all hook-shaped teeth, as opposed to elongate and, often, bifid outer lateral teeth of *B. stellata.* The penial papilla of *B. tamiu* is far more elongate than that of *B. stellata.*

Berthella strongi (MacFarland, 1966), comb. nov.

(Figures 1D, 13, 14)

Pleurobranchus strongi MACFARLAND, 1966:89, pl. 6, figs. 3–7, pl. 15, figs. 1–15, pl. 16, figs. 13, 14.

Distribution: Moss Beach (San Mateo County) to Santa Cruz Island (Santa Barbara County), California (BEHRENS, 1980).

Material: One specimen, CASIZ 064826, intertidal zone, Moss Beach, San Mateo County, California (37°32′N, 122°31′W), 2 August 1966, G. C. Williams and T. M. Gosliner. One specimen, CASIZ 064822, intertidal zone, Great Tide Pool, Pacific Grove, Monterey County, California (36°37′N, 121°54′W), July 1921, F. M. MacFarland.

External morphology: The living animal from Moss Beach (Figure 1D) was approximately 25 mm in length. It was beige with a few scattered opaque white spots. The ctenidium, while simply plicate, has 16 primary pinnae. No obvious tubercles are present along the gill rachis.

Internal morphology: The shell of the specimen from Moss Beach was entirely decalcified and the shell of the specimen from Pacific Grove had been removed by dissection (from MacFarland's notes), but was not with the specimen.

The jaws are ornamented with numerous elements (Figure 13A) bearing 1–5 denticles on either side of the central cusp. The radula has a formula of 62 × 69·0·69 and 61 × 64·0·64 in the two specimens examined. In both cases the innermost teeth (Figure 13B) have a short cusp and are steeply arched. The teeth become more elongate towards the outer margin of the radula, but diminish again in length in the outer 5–7 teeth (Figure 13C). Some secondary denticles were observed in a specimen from Diablo Cove (Figure 13D).

The reproductive system (Figure 14) is androdiaulic and was identical in its configuration in the two specimens examined. The ampulla is straplike and thick. It narrows proximally and divides into the short oviduct and the vas deferens. The female gland mass is well developed, with the mucous gland forming the largest portion of the nidamental glands. The muscular receptaculum seminis is pyriform and possesses an elongate duct. The receptaculum duct joins the vagina near the middle of its length between the large, spherical bursa copulatrix and the gonopore. The vas deferens is prostatic throughout most of its length. The prostate joins with the elongate convoluted penial gland and together they enter the muscular, conical penial papilla.

Discussion: The present material agrees in all respects with MACFARLAND's (1966) and BEHRENS' (1980) descriptions of this species. By virtue of the facts that the gill rachis lacks distinct tubercles and an elongate penial gland is present, this species is transferred from *Pleurobranchus* to *Berthella.*

Berthella strongi is similar to *B. stellata* in several aspects of its morphology. However, there are consistent differences, which clearly differentiate the species. The radular teeth of *B. strongi* (Figure 13) have a narrower, more elongate cusp than any of those found in *B. stellata* (Figures 10, 11). The outer teeth of *B. strongi* are never elongate or bifid. Most significantly, the penial gland of *B. strongi* (Figure 14) is always highly convoluted, while that of *B.*

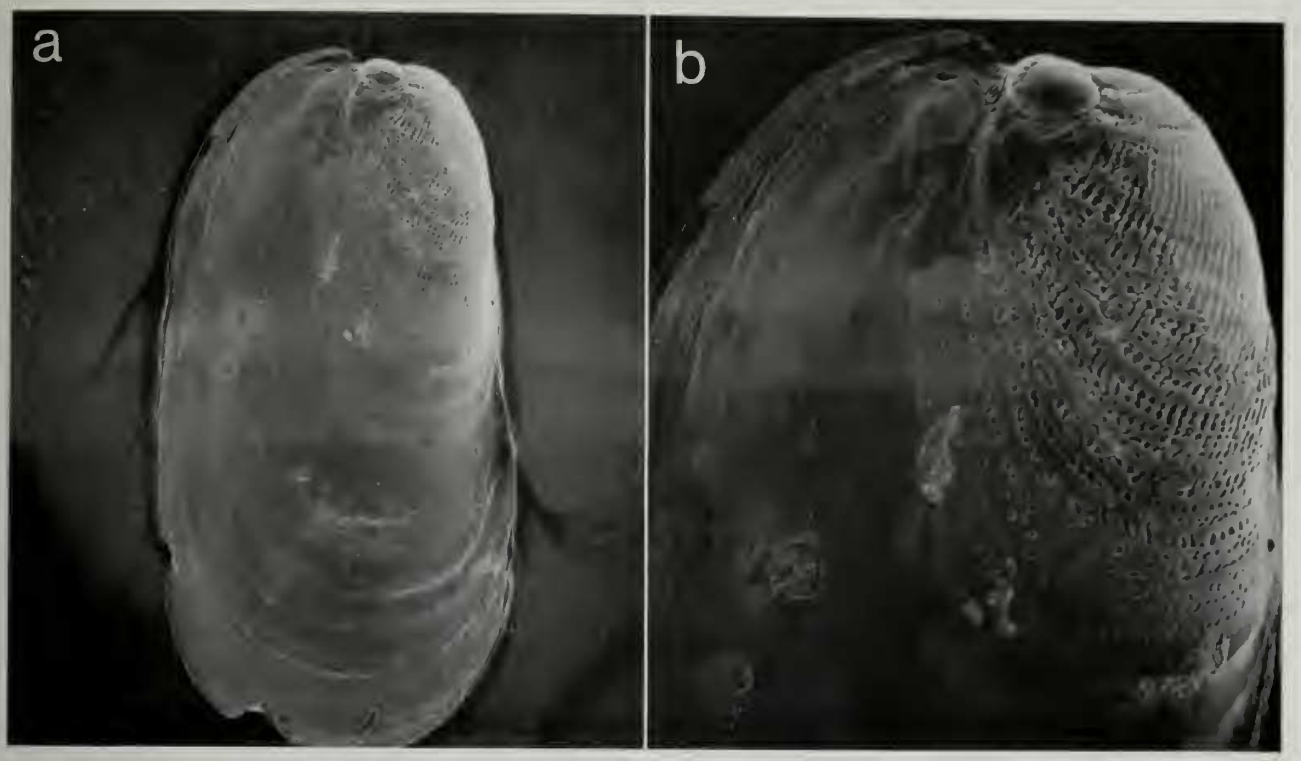

Figure 15

Berthella agassizii (MacFarland, 1909). Scanning electron micrographs of shell of specimen from Campitos, Punta Eugenia, Pacific coast of Baja California Sur. A. Entire shell, ×30. B. Close up of shell showing protoconch and sculpture, ×60.

stellata (Figure 12) has a maximum of one or two convolutions.

Berthella agassizii (MacFarland, 1909)

(Figures 1E, 15–18)

Pleurobranchus agassizii MacFarland, 1909:59, pl. 11, figs. 43–54, pl. 12, figs. 55–57.
Bouvieria agassizii (MacFarland, 1909): Engel, 1927:110, figs. 26a–c.
Berthella agassizii (MacFarland, 1909): Er. Marcus, 1955: 117, figs. 66–77; Ev. Marcus, 1984:51, figs. 6–16.

Distribution: This species has been recorded from several localities within the Caribbean, southwards to Brazil (Ev. Marcus, 1984) and is here recorded from both coasts of Baja California.

Material: Holotype (CASIZ 021162) and paratype (CASIZ 021163) of *Pleurobranchus agassizii,* both collected from Riacho Doce, Alagoas, Brazil, 1899?, A. W. Greely. One specimen, CASIZ 063276, 3 m depth, Campitos, 20 km east of Punta Falsa, Baja California, Mexico (27°50′N, 114°50′W), 30 June 1984, T. M. Gosliner. One specimen, CASIZ 063278, 6 m depth, southern end of Bahía Pulmo, Baja California Sur, Mexico (23°24′N, 109°24′W), 22 January 1984, T. M. Gosliner.

External morphology: The living animals (Figure 1E) reached a maximum of 12 mm in length. The specimen from Campitos was reddish brown with scattered opaque white spots. The individual collected from Cabo Pulmo was translucent pink with scattered opaque white spots. The gill is bipinnate with up to 15 primary pinnae on either side of the central rachis. The anus, in the three specimens examined, is situated on an elevated papilla dorsal to the middle of the gill membrane.

Internal morphology: The shell (Figure 15) is narrow. Only the older portions bear sculpture.

The jaws are well developed with numerous minute elements. The elements (Figures 16A, 17A) bear 1–6 denticles on either side of the central cusp.

The radular formula is 45–52 × 42–53·0·42–53 in three specimens examined. The inner lateral teeth (Figures 16B, 17B, C) are simply hook-shaped, without auxiliary denticles. The middle teeth of each half row (Figure 16C) are larger, but essentially the same shape as the inner teeth. The outermost teeth (Figures 16D, 17D) are simple, small hooks, without a secondary denticle.

The reproductive system (Figure 18) is androdiaulic. The thick, slightly convoluted ampulla narrows distally and divides into the short oviduct and an elongate, prostatic vas deferens. The vas deferens narrows prior its junction

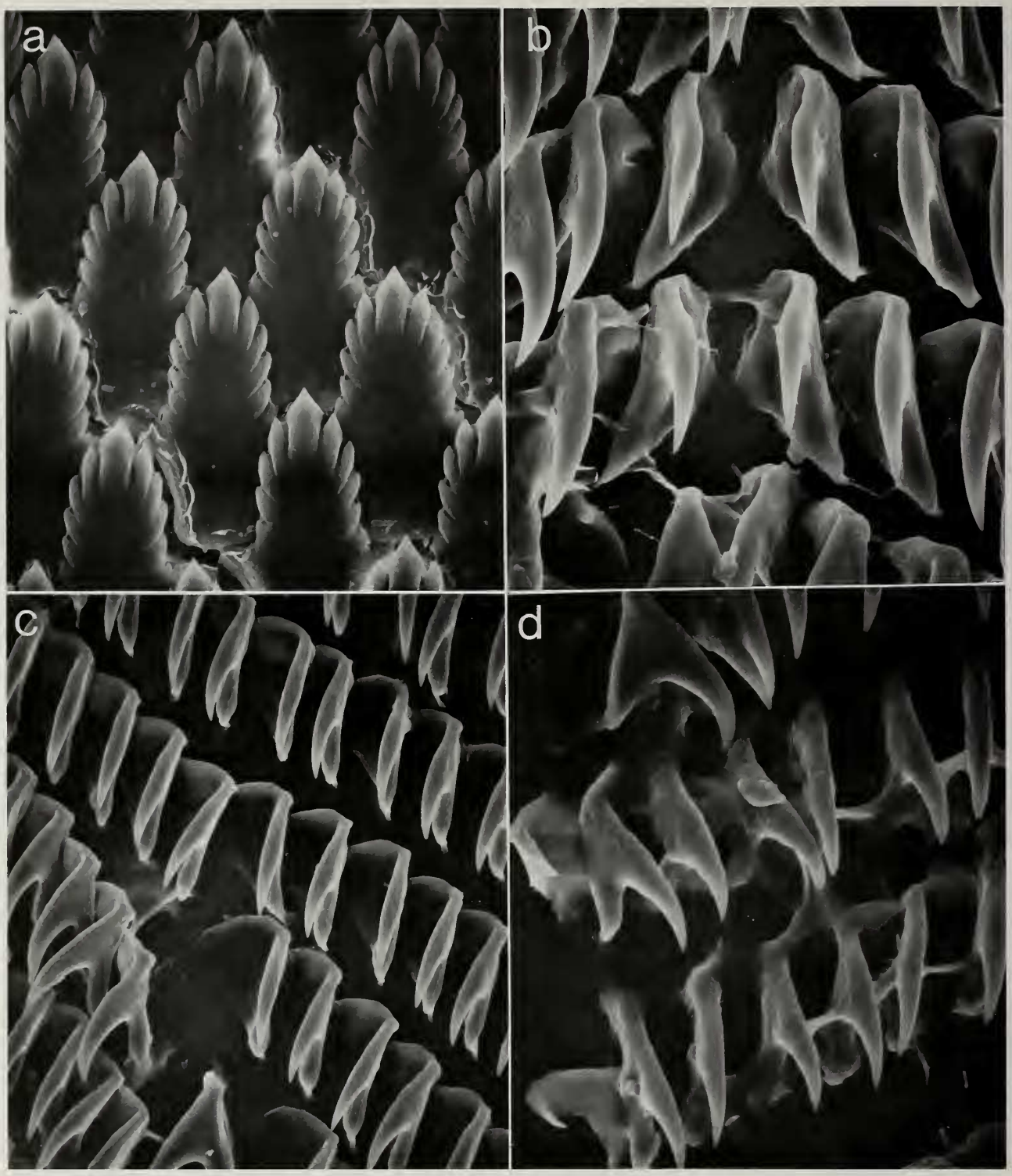

Figure 16

Berthella agassizii (MacFarland, 1909). Scanning electron micrographs of paratype. A. Jaw elements, ×2000. B. Inner lateral radular teeth, ×1300. C. Middle lateral radular teeth, ×800. D. Outer lateral teeth, ×1100.

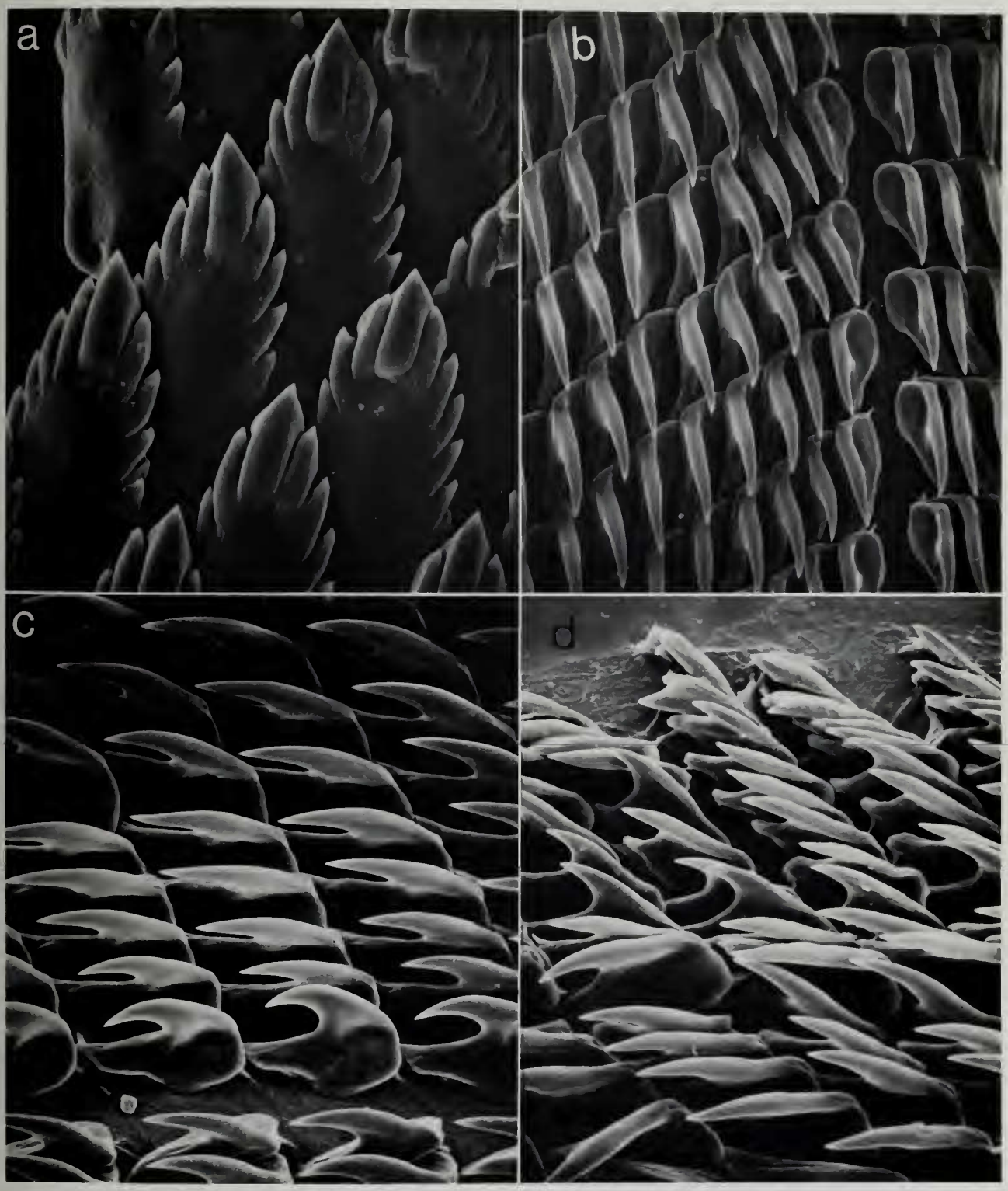

Figure 17

Berthella agassizii (MacFarland, 1909). Scanning electron micrographs of specimen from Campitos, Pacific coast of Baja California Sur, Mexico. A. Jaw, ×2000. B. Dorsal view of inner lateral teeth, ×800. C. Lateral view of inner lateral teeth, ×1200. Outer lateral teeth, ×1280.

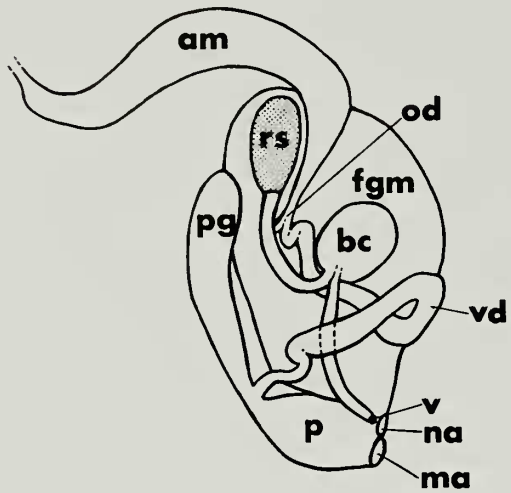

Figure 18

Berthella agassizii (MacFarland, 1909). Reproductive system of specimen from Campitos, Baja California Sur, Pacific coast of Mexico: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; ma, male aperture; na, nidamental aperture; od, oviduct; p, penis; pg, penial gland; rs, receptaculum seminis; v, vagina; vd, vas deferens.

with the penial gland. The penial gland is slightly curved, but not convoluted. The penial papilla is short and conical within a bulbous male atrium. In all four specimens examined, one each from both coasts of Baja California (present study), the paratype of *Berthella agassizii* from Brazil (present study) and from an unspecified locality in the Caribbean (Ev. Marcus, 1984, as *B. agassizii*), the receptaculum seminis contains black pigment internally. Even in MacFarland's specimen, collected in 1899, traces of pigment are still present in the receptaculum. The duct of the receptaculum joins the vagina either at the base of the spherical bursa copulatrix or in the middle of the vaginal duct.

Discussion: *Berthella agassizii* is sympatric with the circumtropical *B. stellata* within the Caribbean (Ev. Marcus, 1984) and along both coasts of Baja California (present study).

The two species differ consistently in several aspects of their external and internal morphology. *Berthella agassizii* has a reddish or pink notum, while that of *B. stellata* is translucent white or honey colored. The opaque white markings of *B. agassizii* are small spots and never form the broad crosses characteristic of *B. stellata*. In *B. agassizii*, the anus is situated near the middle of the gill membrane, while in *B. stellata* it is at the posterior limit of the gill.

The radular teeth of *Berthella agassizii* are uniformly hook-shaped, while in *B. stellata* the outermost teeth are elongate with a secondary denticle.

The reproductive system of *Berthella agassizii* differs from that of *B. stellata* in two significant regards. In *B. agassizii* the receptaculum seminis contains dark pigment, while that of *B. stellata* is unpigmented. In *B. agassizii* the penial sac is proportionally larger than in *B. stellata*.

DISCUSSION

Until recently, generic differences within the notaspideans have long been the source of considerable confusion. Much of this confusion stems from the fact that many external characters, such as the relative proportions of the mantle and foot, have been shown to be artifacts of preservation (Ev. Marcus & Gosliner, 1984; Willan, 1984). Also, the shape of jaw elements and radular teeth varies within a population, or even within a single individual.

There has been considerable confusion surrounding the separation of *Pleurobranchus* from *Berthella*. *Pleurobranchus* had been separated from *Berthella* by its tuberculate ctenidium and by having a diaulic rather than triaulic arrangement of reproductive organs.

Recently, Willan (1987) has revised the notaspidean genera, based on a cladistic analysis of morphological characters. He demonstrated that gill tuberculation and diauly versus triauly are useful in separating *Pleurobranchus* from *Berthella*. He also noted additional characters that are useful in separating *Berthella, Bathyberthella, Berthellina,* and *Pleurehdera* (tribe Berthellini) from their sister taxon, *Pleurobranchus*. Living *Pleurobranchus* pulsate the rhinophores. This may be an adaptation for increasing respiration in these large, active animals. Members of *Pleurobranchus* also have prominent flaps surrounding the genital apertures.

It should be noted that the triaulic arrangement of reproductive ducts present in the genera *Berthella, Pleurehdera, Bathyberthella,* and *Berthellina* is fundamentally different from that of doridacean nudibranchs. In dorids, the uterine duct connects the receptaculum seminis and bursa copulatrix with the female gland mass. In these triaulic notaspideans, a uterine duct is absent and the only connection of the receptaculum and bursa with the female gland mass is at the common genital atrium.

The genus *Pleurehdera* Marcus & Marcus, 1970b, was established to accommodate *P. haraldi* Marcus & Marcus, 1970b. It differs from *Berthella* by having bifid radular teeth. Willan (1987) noted that it is the most poorly differentiated notaspidean genus and suggested that it is allied to *Berthellina*. The fact that the presence of bifid teeth may vary within a single species (*Berthella stellata*, present study) indicates that this character, alone, cannot be used for generic separation. Willan (1987) noted that the shell of *Pleurehdera* is larger than that present in *Berthellina*, and is therefore more similar to the shell of *Berthella*. *Berthellina* also possesses elongate radular teeth with multiple denticles along their length. The radular teeth of *Pleurehdera haraldi* (Willan, 1984:fig. 1) are virtually identical to those seen in some specimens of *Berthella stellata* (Figure 11). On this basis, further study of *Pleurehdera* must be undertaken to re-examine its systematic placement and relationship to *Berthella* and *Berthellina*. Although considerable morphological variability has been previously

reported within the Pleurobranchidae, we have found that two widespread species, *Berthella stellata* and *B. martensi*, are among the most variable species of notaspideans. Much of the range of variation is present within single populations of these species.

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